PRAIRIE INCLUSIONS IN THE DECIDUOUS FOREST CLIMAX

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INTRODUCTION

In the deciduous forest of the central states small fragments of prairie frequently occur (see fig. 1). These vary in area from a few square feet to several acres, occurring usually on hillsides exposed to the south, southeast, or southwest. Shimek (5, 6, 7) has noted them in northwestern Iowa and along the Missouri River; Pammel, MacDonald, and Clark (2) along the Missouri River in Iowa; Vestal (8) in Illinois; Pool, Weaver, and Jean (3) in southeastern Nebraska, and the writer in the vicinity of Cincinnati, Ohio. During the spring and summer of 1917, near Peru, in southeastern Nebraska, the writer studied intensively two small inclusions in relation to the surrounding forest. The data collected in this study are important in explaining the occurrence of prairie inclusions.

GENERAL DESCRIPTION OF THE REGION

From the broad lowlands of the Missouri River in southeastern Nebraska arise abruptly densely wooded hills and bluffs, broken by numerous valleys and ravines. The forest of this hilly region is of the red oak-hickory type. It varies greatly in width, but in the fairly level upland soon gives way to the prairie. Pound and Clements (4) and Pool, Weaver, and Jean (3) have studied and described this forest in detail. The latter have shown by instrumental and quadrat studies that the succession from grassland is through the following stages: shrub, *Quercus macrocarpa–Q. acuminata*, *Q. velutina*, *Q. rubra–Hicoria ovata*, which is dominant in fairly mesophytic situations, and the final stage, *Tilia americana–Ostrya virginiana*, which is dominant on the moister slopes and in ravines.

A striking feature of this hilly forest region is that often on the sides and tops of the steep slopes and on the crests of ridges in the midst of the dense forest are found prairie areas varying from a few square feet to an acre or more. These fragments of prairie are usually found on south, southeast, or southwest slopes, directly exposed to the sun and to the wind which is prevailingly from the south from April 1 to October 1. The vegetation of the fragments is composed of typical prairie plants. The following grasses, forming well-defined bunches, are dominant: *Andropogon furcatus* Muhl., *Schizachyrium scoparium* (Michx.) Nash, *Sorghastrum nutans* L., and *Atheropogon curtipendulus* (Michx.) Fourn. Between the bunches are found numerous typical prairie herbs and occasionally a few shrubs.

Description of the Stations

One of these fragments was selected for detailed study (fig. 1). It was located on a very steep south slope surrounded on all sides by a dense forest composed of *Quercus rubra*, *Q. velutina* Lam., *Hicoria ovata*, *H. cordiformis* (Wang.) Britton, *Ulmus fulva* Michx., *Tilia americana* L., and others. The northern slope of the ridge on which this fragment was located was just as steep as the southern slope, but it was forested. Between the forest and the prairie was a narrow zone of shrubs, often denser than the forest itself.

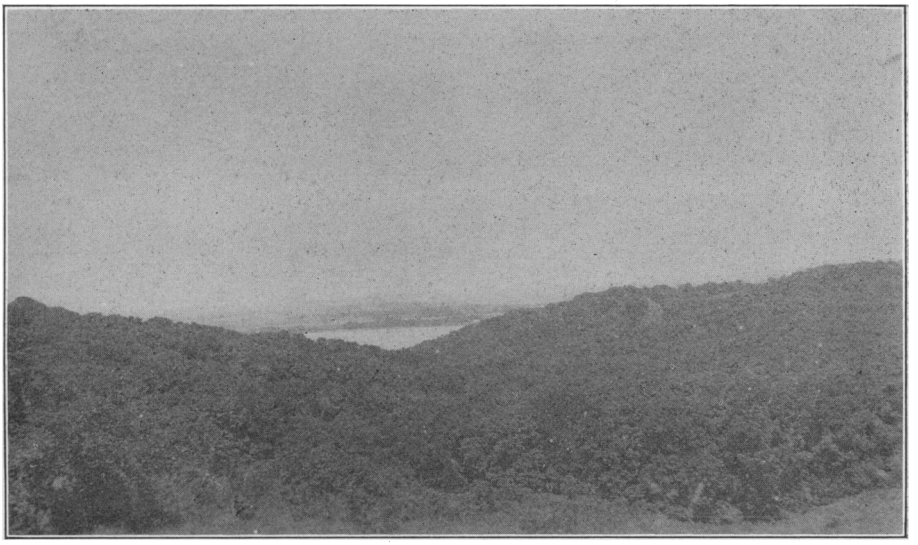

FIG. 1. Deciduous forest in southeastern Nebraska, where prairie inclusions occur.

The chief shrubs in this zone were *Rhus glabra* L., *Cornus femina* Mill., *Zanthoxylum americanum* Mill., *Symphoricarpos symphoricarpos* (L.) MacM., *Salix humilis* Marsh., and *Toxicodendron radicans* (L.) Kuntze; and the vine *Celastrus scandens* L. was very frequently encountered. Seedlings and saplings of *Quercus macrocarpa*, *Q. muhlenbergii* Engelm., *Ulmus fulva*, and *Hicoria cordiformis* were also frequent in this zone. A narrow and poorly defined zone of *Quercus macrocarpa*, *Ulmus fulva*, and *Q. muhlenbergii* was found in places between the shrub and red oak-hickory forest. In the prairie the four bunch grasses were dominant. The principal herbs, *Petalostemum candidum* (Willd.) Michx., *P. purpureum* (Vent.) Rydb., *Lithospermum linearifolium* Goldie, *L. carolinense* (Walt.) MacM., *Astragalus missouriensis* Nutt., *Verbena stricta* Vent., *Laciniaria punctata* (Hook.) Kuntze, and *Solidago* sp., and the shrubs, *Rhus glabra* and *Toxicodendron radicans*, were scattered, especially over the lower part of the slope; *Ceanothus ovatus* Desf. and *Amorpha canescens* Pursh were scattered, and a clump of

Salix humilis occurred on the upper part of the slope. Dead bur oaks and shrubs, from one to five feet high, were scattered sparsely over the slope. It seemed probable that these were killed by a more xerophytic period following a more mesophytic one in which they had developed. A few bur-oak seedlings were found, but the small leaves, the dryness, and often the yellowish-red color of the plants showed the effects of their hard struggle.

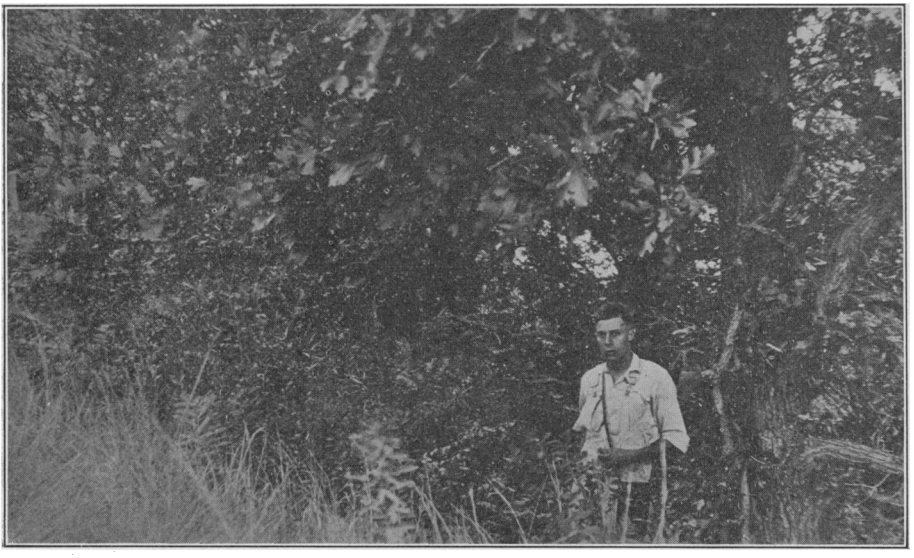

FIG. 2. Portion of a prairie inclusion showing sharp transition to forest.

Two stations were selected in the prairie fragment described above and four in the shrubs and woods surrounding this fragment. Later in the summer two more stations were selected to study another fragment. One of the prairie stations in the first remnant was located near the summit of the slope, another near the shrubs at the base, called respectively "high prairie" and "low prairie" in the following discussion. Two shrub stations were located on the gentle slope of the narrow shrub zone at the base of the remnant, and about two meters from the edge of the prairie. The shrub stations were about ten meters apart. In one, Cornus and young *Quercus macrocarpa* were dominant, while in the other *Zanthoxylum americanum*, Cornus, and *Toxicodendron radicans* were dominant. The red oak-hickory forest station was located about fifteen meters from the base of the prairie. The most abundant tree was *Quercus rubra*, while *Hicoria cordiformis* and *Ulmus fulva* occurred frequently. The luxurious undergrowth consisted of *Quercus rubra*, *Ulmus fulva*, *Cercis canadensis* L., *Hicoria cordiformis*, *Tilia americana*, *Parthenocissus quinquefolia*, *Toxicodendron radicans*, and *Symphoricarpos symphoricarpos*. The bur-oak forest station was

located on the very steep north slope, just below the shrubs, which formed a zone extending for two or three meters in width from the crest. The dominant tree was *Quercus macrocarpa; Ulmus fulva*, *Hicoria cordiformis*, *Toxicodendron radicans*, *Parthenocissus quinquefolia*, and *Celastrus scandens* formed the open undergrowth. The shrubs in the zone between this forest and the prairie were *Rhus glabra*, *Cornus femina*, *Zanthoxylum americanum*, *Symphoricarpos symphoricarpos*, and *Toxicodendron radicans*.

Factor Readings

1. Evaporation

The evaporating power of the air was measured from May 10 to September 7 in the above-described stations by means of Livingston's standardized cylindrical atmometers without rain correctors. The table gives the average daily evaporation for the periods between readings and the daily average for the entire season.

Table 1. *Daily Amounts of Evaporation during Periods between Readings, and the Daily Average for the Season: Peru, Nebraska, 1917*

Period	High Prairie	Low Prairie	Dogwood-Bur Oak Shrub	Prickly Ash-Dogwood Shrub	Red Oak-Hickory Forest	Bur-Oak Forest
May 10–18.....	33.0 cc.	31.5 cc.	21.7 cc.	25.6 cc.	22.7 cc.	24.7 cc.
May 18–26.....	17.8	14.4	10.0	9.4	8.3	10.5
May 26–June 2....	5.4	2.4	1.7	1.1	1.8	2.3
June 2–12.....	12.7	8.8	5.3	4.8	4.2	4.9
June 12–19.....	25.0	24.6	13.2	13.7	11.8	13.4
June 19–July 4....	16.0	15.7	7.2	8.8	7.0	8.2
July 4–10.....	16.1	16.3	6.8	6.8	6.8	7.2
July 10–17.....	18.4	15.3	8.3	8.1	7.6	8.3
July 17–26.....	22.9	20.0	7.2	6.6	5.8	8.2
July 26–Aug. 2....	40.6	36.2	23.7	21.4	18.2	22.0
Aug. 2–9	14.4	9.8	4.8	5.7	3.7	4.8
Aug. 9–16.....	18.2	14.0	5.4	5.0	4.2	5.2
Aug. 16–22.....	13.8	9.2	3.1	3.1	3.3	4.2
Aug. 22–31.....	26.1	19.1	10.6	9.9	9.7	11.2
Aug. 31–Sept. 7...	20.5	16.2	6.3	7.2	5.9	8.1
Daily average May 10–Sept. 7.....	20.6	16.9	9.0	9.1	7.9	9.5

The table shows that the evaporation for the season was greatest in the high prairie with 20.6 cc. daily average loss, next in the low prairie with 16.9 cc., followed by bur-oak forest with 9.5 cc., shrubs with 9.1 cc., and least in the red oak-hickory forest with 7.9 cc. The greatest evaporation occurred in the high prairie because this station was more directly exposed to the sun and wind. The bur-oak forest station showed a greater evaporation loss than the shrub stations because the growth was much more open in the former, thus allowing freer circulation of the air and reducing to a

less extent the light intensity. The shrub zone was so dense in many places that passage through it was almost impossible; such places did not occur in the bur-oak forest. The evaporation was lower in the low prairie than in the high prairie because it was less exposed to the sun and wind, it was in the shade later in the morning and earlier in the evening, and it retained the dew longer.

2. Soil Moisture

Soil moisture readings were taken eight times from May 18 to July 19 at depths from 0 to 10 cm. and 10 to 30 cm. in each of the six stations where the atmometers were operated. These readings, with wilting coefficients for three of the stations, are given in table 2.

At both depths, 0–10 cm. and 10–30 cm., the readings show with striking regularity that the high prairie had the lowest soil moisture, this increasing in the stations in the following order: low prairie, bur-oak forest, shrubs and red oak-hickory forest. Water was unavailable for plant growth in the

TABLE 2. *Total Water Content of the Soil at Depths of 0–10 cm. and 10–30 cm. in Various Stations at Peru, Nebraska, 1917*

Station	May 18	May 26	June 2	June 12	June 19	July 4	July 15	July 29	Average	Wilting Coefficient
0–10 cm.	%	%	%	%	%	%	%	%	%	%
High prairie.....	8.9	23.3	26.6	15.1	7.3	12.5	15.8	5.4	14.5	13.0
Low prairie.....	12.8	15.5	28.4	18.7	9.0	15.0	18.4	6.6	15.5	
Dogwood-bur oak shrub.....	19.8	28.3	32.9	25.9	16.8	22.6	24.0	11.4	22.7	
Prickly ash-dogwood shrub....	23.1	32.1	33.9	29.9	18.7	23.5	25.9	14.5	25.2	
Red oak-hickory forest.....	32.7	37.1	38.5	34.0	27.9	33.0	30.9	15.7	31.2	15.5
Bur-oak forest...	16.9	27.1	31.0	24.0	16.2	21.9	19.6	9.8	20.8	15.2
10–30 cm.	%	%	%	%	%	%	%	%	%	%
High prairie.....	13.3	19.8	23.5	18.3	11.7	16.1	12.0	6.7	15.2	11.9
Low prairie.....	15.3	22.3	26.2	21.5	12.7	16.3	13.2	8.5	17.0	
Dogwood-bur oak shrub.....	20.1	26.9	31.1	25.4	19.4	22.8	19.6	15.1	22.5	
Prickly ash-dogwood shrub....	24.6	29.1	31.3	27.7	22.1	24.0	23.5	15.3	24.7	
Red oak-hickory forest.....	28.5	31.2	36.0	30.8	25.3	28.9	25.1	16.4	27.8	12.5
Bur-oak forest...	20.1	24.8	28.5	23.1	18.7	21.8	17.2	11.7	20.7	12.5

high prairie at 0–10 cm. four times and at 10–30 cm. two times during the growing season. In the bur-oak station it was unavailable once at both depths. Water was available for growth in the red oak-hickory station at all readings. The low water content in the high prairie was caused by the direct exposure to sunlight and wind, and by the great amount of run-off caused by the steepness of the slope. The bur-oak forest had a lower soil water content than the shrub stations because the plant cover was less dense.

Discussion

The maintenance of prairie inclusions against invasion by the shrub and the forest by which they are surrounded has been discussed by a few writers. Shimek (7) states that the chief factor is the exposure to evaporation as determined by temperature, wind, and topography. He believes that the "determining causes of relative prairie and forest distribution evidently lie in the atmosphere rather than in the soil" (7, p. 24), and that prairie fire was an effect rather than a cause. Vestal (8, pp. 122, 123) says:

> The essential condition is the great insolation and exposure to the dry summer winds from the south and southwest, making for local xerophytism. This is apparently a static rather than a dynamic feature of the environment, since both habitat and xerophytic vegetation may persist indefinitely, even though there is a slow lateral migration as the valley widens. It is probable that the dryness occasioned by the slope to the south is in most places not in itself sufficient to preserve the prairie from forest encroachment, for forest is able to establish itself in quite xerophytic habitats in the vicinity, and has in fact done so over most of the south-facing ravine slopes. Other physical factors aid in the original exposure afforded by direction of slope. One is instability of surface, due partly to steepness, partly to the meagerness of protection against erosion afforded by the open and sparse ground-cover. Others are accidental and artificial factors which destroy or check forest growth, such as fire, cutting, grazing, and trampling. These operate in places only temporarily, but in other places recur frequently enough to permit the continued existence within the forest of small but rather numerous patches of prairie, with more or less shifting boundaries, wherever the basic condition of southward exposure is fairly extensive.

Pool, Weaver, and Jean (3), in studying the vegetation in the vicinity of Peru, Nebraska, collected considerable factor data on a rather large prairie fragment. They state (p. 27) that

> Except for fires, grazing or other disturbance much of this subclimax grassland would undoubtedly pass through a scrub stage in succession and culminate in forest while still other extensive areas would probably remain covered with chaparral.

But in the summary they state that

> The high saturation deficit and low soil moisture content (often reaching the non-available point) of the prairie sites in eastern Nebraska constitute barriers over which the forest trees can scarcely pass. We probably have herein the most ready explanation as to why our natural Nebraska woodlands are confined to the moist slopes of rather narrow valleys, and also the most probable answer to the oft-repeated question as to the treelessness of the prairies in general [p. 47].

The factors given for the maintenance of prairie areas are: *A*, Climatic: (1) temperature, by increasing evaporation; (2) wind, by increasing evaporation and by mechanical effect on tissues; (3) light (insulation) causing greater evaporation. *B*, Edaphic: (4) topography, steepness of the slope causing instability of the soil; (5) low water content. *C*, Biotic and accidental: (6) fire; (7) grazing and trampling; (8) cutting.

It does not appear that fire, grazing, trampling, or cutting is an important factor in the maintenance of these small prairie inclusions, because on

account of their isolation within the deep forest these factors as a rule do not affect them. The steepness of the slope would cause some washing of fruits and seeds and young plants; but in depressions and among the prairie shrubs and grass bunches there would be adequate protection from washing. Seedling trees and shrubs occur, as reported by Pool, Weaver, and Jean and by the writer, in spite of the washing.

The data presented in this paper and in the paper by Pool, Weaver, and Jean appear to prove that the dryness of the air, caused by the direct exposure to sunlight and wind, and the low water content of the soil, caused by the high evaporating power of the air and the run-off due to the steep slope, are the determining factors in the maintenance of the prairie inclusions against forest invasion. The air near the surface of the prairie is usually two to four times as dry as in the surrounding shrubs and woods. The water content of the first foot of soil frequently falls below the non-available point in the prairie, while this rarely happens in the shrub and forest. In the prairie, conditions for the germination of tree and shrub seeds are usually not favorable. In case the seeds do germinate, the seedlings are frequently exposed to very dry air and to non-available soil water. The sickly appearance of the tree seedlings observed in the prairie may be accounted for in this way.

Summary

1. Prairie inclusions have been reported as occurring in the deciduous forest climax in Ohio, Illinois, Iowa, and eastern Nebraska.

2. This paper presents the results of an intensive study of a small prairie inclusion near Peru, in southeastern Nebraska.

3. The evaporating power of the air was measured by Livingston standardized atmometers. The daily average losses from May 10 to September 7 were: high prairie (near summit of steep slope) 20.6 cc., low prairie (near base of steep slope) 16.9 cc., shrub zone at base of prairie slope 9.0 cc., red oak-hickory forest below the shrub zone 7.9 cc., bur-oak forest near summit of north slope 9.5 cc.

4. The average of eight total soil-water content readings, at 0–10 cm. depth, from May 18 to July 29 were: high prairie 14.5 percent (wilting coefficient 13.0 percent), low prairie 15.5 percent, shrubs 23.8 percent, red oak-hickory forest 31.2 percent (wilting coefficient 15.5 percent), bur-oak forest 20.8 percent (wilting coefficient 15.2 percent). For the depth of 10–30 cm. the averages were: high prairie 15.2 percent (wilting coefficient 11.9 percent), low prairie 17.0 percent, shrubs 23.6 percent, red oak-hickory forest 27.8 percent (wilting coefficient 12.5 percent), bur-oak forest 20.7 percent (wilting coefficient 12.5 percent).

5. The data presented in this paper tend to prove that the chief factors in the maintenance of the prairie inclusions from invasion by the surrounding shrubs and trees are the great evaporating power of the air caused by

exposure to sunlight and prevailing winds, and the low soil-water content, often falling below the available point.

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BIBLIOGRAPHY

1. **Meyer, A. H., et al.** Soil survey of Nemaha County, Nebraska. U. S. Dept. Agr., Bur. Soils. Pp. 38. 1916.
2. **Pammel, L. H., MacDonald, G. B., and Clark, H. B.** The native and cultivated forest trees and shrubs of the Missouri River basin. Proc. Ia. Acad. Sci. **22** : 23–56. 1915.
3. **Pool, R. J., Weaver, J. E., and Jean, F. C.** Further studies in the ecotone between prairie and woodland. Univ. Nebr. Stud. **18** : 1–47. 1918.
4. **Pound, R., and Clements, F. E.** The phytogeography of Nebraska. Lincoln, Nebraska, 1900.
5. **Shimek, B.** Geology of Harrison and Monona Counties. Botanical Report Ia. Geol. Surv. **20** : 426–485. 1911.
6. ——. The prairies. Bull. State Univ. Ia. 6^2 : 169–240. 1911.
7. ——. The plant geography of the Lake Okoboji region. Bull. State Univ. Ia. 7^2: 3–69. 1915.
8. **Vestal, A. G.** Local inclusions of prairie within forest. Trans. Ill. Acad. Sci. **11** : 122–126. 1918.